ON TWO ADVANCED CARNIVOROUS CYNODONTS FROM THE LATE TRIASSIC OF SOUTHERN BRAZIL

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ABSTRACT. Cranial and postcranial remains of the cynodonts *Therioherpeton cargnini* (Therioherpetidae) and a taxon originally referred to as *Thrinaxodon brasiliensis* (of indeterminate familial status) are described and compared with other advanced cynodonts and morganucodontids. Our study provides evidence that these early Late Triassic cynodonts, which possessed primitive carnivorous dentitions of the *Thrinaxodon liorhinus* type, evolved derived characters of the skull and postcranium that approximated the mammalian level of organization as represented in morganucodontids.

INTRODUCTION

Therioherpeton cargnini (Therioherpetidae) is represented by an incomplete skull and lower jaw, and most of the postcranial skeleton, but only the skull and a fragment of the lower jaw have been described (Bonaparte and Barberena, 1975). The genus *Therioherpeton* was referred to the family "Therioherpetontidae" by Bonaparte and Barberena (1975), but Battail (1991) corrected the familial name to Therioherpetidae. Likewise, *Thrinaxodon brasiliensis* (Barberena et al., 1987), of indeterminate familial status, is also represented by an incomplete skull, lower jaws, and some postcranial bones, but only the skull and jaws were described. In this paper the complete material known from both species is analyzed and compared with other advanced Triassic cynodonts and mor-

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ganucodontids, and *T. brasiliensis* is assigned to a new genus. The advanced anatomical features of both taxa suggest a close proximity to the mammalian condition, not very different from that evolved by tritylodontids and tritheledontids.

Anatomical and phylogenetic issues concerning advanced cynodonts and primitive mammals have been widely analyzed (Kermack et al., 1981; Kemp, 1982; Jenkins, 1984; Crompton and Sun, 1985; Sues, 1985; Hopson and Barghusen, 1986; Battail, 1991; Hopson, 1991; Shubin et al., 1991; Crompton and Luo, 1993; Luo, 1994), but the subject is far from well understood because, as Crompton and Luo (1993: 30) remarked: "A lack of morphological information makes it difficult to interpret the relationships of advanced cynodonts and early mammals." As yet undescribed carnivorous cynodonts (recently discovered in southern Brazil in beds of early Late Triassic age), and a restudy of the advanced cynodonts *Therioherpeton cargnini* (Bonaparte and Barberena, 1975) and *Thrinaxodon brasiliensis* (Barberena et al., 1987), may advance our understanding of the complex sequence of anatomical changes that occurred in cynodonts and that foreshadow the level of mammalian organization represented by morganucodontids (Kermack et al., 1973, 1981; Crompton, 1974; Jenkins and Parrington, 1976; Gow, 1986). Unfortunately, available cranial material of neither *Thrinaxodon brasiliensis* nor *Therioherpeton cargnini* includes critical anatomical data from the basicranial region.

SYSTEMATIC PALEONTOLOGY

Therapsida Broom, 1905

Cynodontia Owen, 1861

Family Therioherpetidae Bonaparte and Barberena, 1975

Diagnosis. Differs from the Thrinaxodontidae by a more extensive secondary palate. Differs from Thrinaxodontidae, Cynognathidae, Chiniquodontidae, and Probainognathidae in the following features: triangular cross section of the zygomatic arch; absence of a postorbital bar; frontal borders the orbit and bears an anterolateral projection that contacts a lateral portion of the nasal; interorbital wall more highly ossified; larger size of the neural canal in the cervical and dorsal vertebrae; parallel dorsal and ventral borders of the ilium; convex lateral surface of ilium; a narrow, elongate neck of the ischium; obturator foramen relatively large; greater trochanter of the femur extends to the same proximal level as the femoral head. Therioherpetidae differs from Tritheledontidae in the transverse narrowness of the upper postcanines. Therioherpetidae differs from gomphodont cynodonts, including Tritylodontidae, in possessing triconodont upper and lower postcanines, and in the triangular cross section of the zygomatic arch. Therioherpetids differ from basal mammals in lacking an articular condyle of the dentary and fully bifurcated roots on postcanine teeth (but see Shapiro and Jenkins, 2001).

Genus *Therioherpeton* Bonaparte and Barberena, 1975

Type Species *Therioherpeton cargnini* Bonaparte and Barberena, 1975

Holotype. An unnumbered specimen in the private collection of the Patronato Alves Ramos, Santa Maria City, State of Rio Grande do Sul, Brazil. An incomplete skull lacking the basicranium, and preserving only the right upper fifth postcanine; a fragment of the right dentary; an isolated lower postcanine (the fifth or sixth, attached to lingual surface of Pc[5]); 29 articulated, incomplete vertebrae including 4 cervicals, 15 dorsals and (separated by a gap) 4 sacral and 6 caudal vertebrae; associated, incomplete ribs; left scapular blade; distal half of the right humerus; incomplete right radius and ulna; incomplete ilia; complete pubis; right ischium; complete left and incomplete right femur; fragments of tibiae and fibulae; and incomplete feet.

Revised Generic and Specific Diagnosis. The triconodont upper and lower postcanines are without cingula. The secondary bony palate extends nearly to the level of the last postcanine, as in chiniquodontids and *Probainognathus.* As in *Morganucodon,* the frontals have an extensive posterior projection, anteriorly contact the lateral aspect of the nasals, and anterolaterally project to the lacrimals. Prefrontals and postorbitals are absent. The cervical vertebrae are craniocaudally short, transversely wide, dorsoventrally low, and exhibit a very large neural canal. The iliac blade lacks a posterior projection, the lateral surface is convex, and the dorsal and ventral borders are subparallel. The obturator fenestra is large. The greater trochanter extends proximally to the level of the femoral head, with which it is connected by a sheet of bone.

Horizon and Locality. Upper Santa Maria Formation. A road cut on the BR-216 highway (outcrop BR-14 in Bortoluzzi and Barberena, 1967), 200 m northwest of Cerriquito, Township of Santa Maria, Rio Grande do Sul, Brazil.

Age. Probably early Late Triassic.

DESCRIPTION

Skull (Figs. 1–4). Only the salient characters of the type and only known skull of this species, originally described by Bonaparte and Barberena (1975), may be noted here. The more significant characters are the absence of the prefrontal and postorbital, the large lacrimal, the frontal bordering the orbit with a long posterior pro-
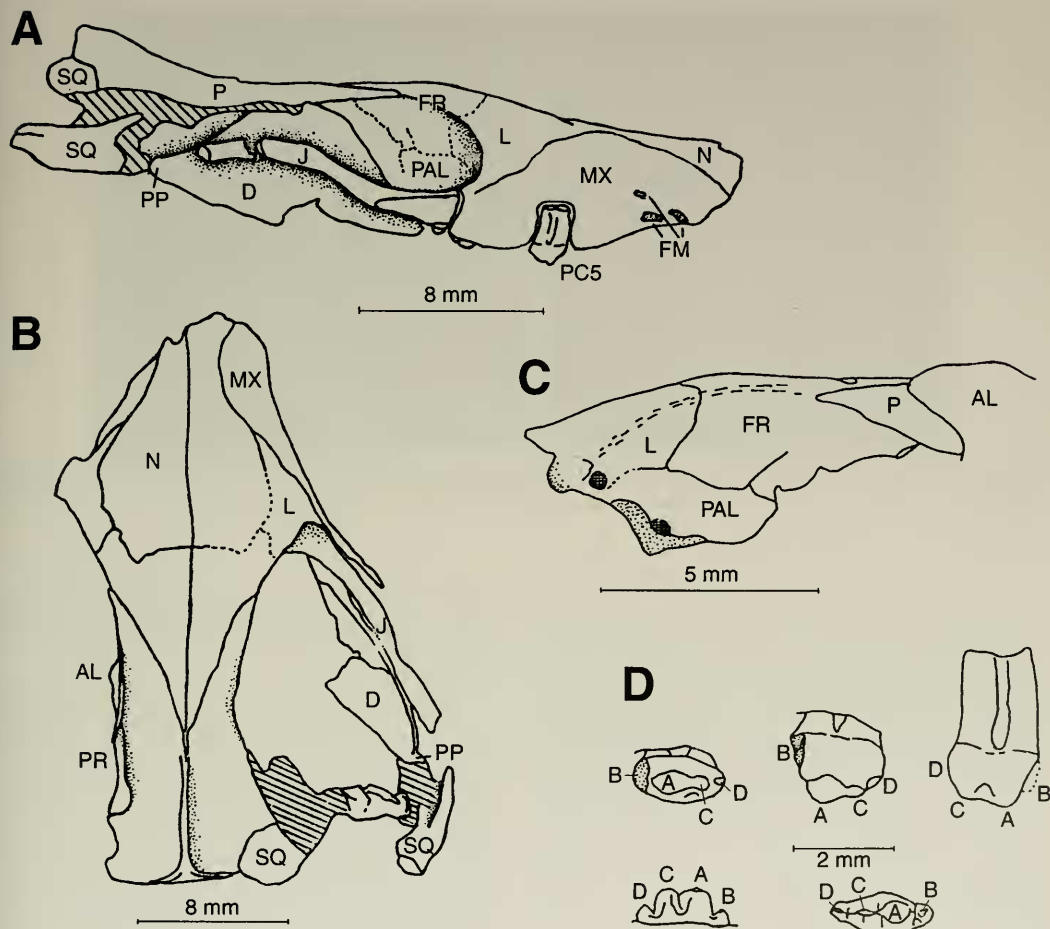
Figure 1.   *Therioherpeton cargnini.* Skull and dentary fragment in (A) right lateral and (B) dorsal views. (C) Incomplete interorbital wall viewed from the left side. (D) Upper postcanine 5 in occlusal, lingual, and buccal views, and $Pc_{5 \text{ or } 6}$ in buccal and occlusal views. *Abbreviations:* AL, alisphenoid; D, dentary; FM, maxillary foramina; FR, frontal; J, jugal; L, lacrimal; MX, maxilla; N, nasal; PAL, palatine; P, parietal; PP, prearticular process; PR, prootic; SQ, squamosal.

cess, and an anterolateral projection of the frontal in dorsal view. The parietal crest is low (Fig. 1A) and the dorsal area of the braincase is large (Fig. 3); the zygomatic arch is slender with a triangular cross section (Figs. 1A, 4). The lateral surface of the maxilla bears three large foramina (Fig. 1A). The upper and lower postcanines (Fig. 1D) are of the triconodont type and lack cingula, and the upper teeth show clear indications of an incipient bifurcation of the roots.

The secondary bony palate of *Therio-*

herpeton was misinterpreted by Bonaparte and Barberena (1975) because an unossified, or damaged, area of the right palatine was considered as part of the internal nares. Restudy of the palatine revealed that its posterior margin is in fact complete, and thus represents the posterior border of the secondary bony palate, which is in line with the penultimate postcanine (Fig. 2).

Postcranial Skeleton (Figs. 5–8). The associated postcranium was found in nearly articulated condition lying on the external
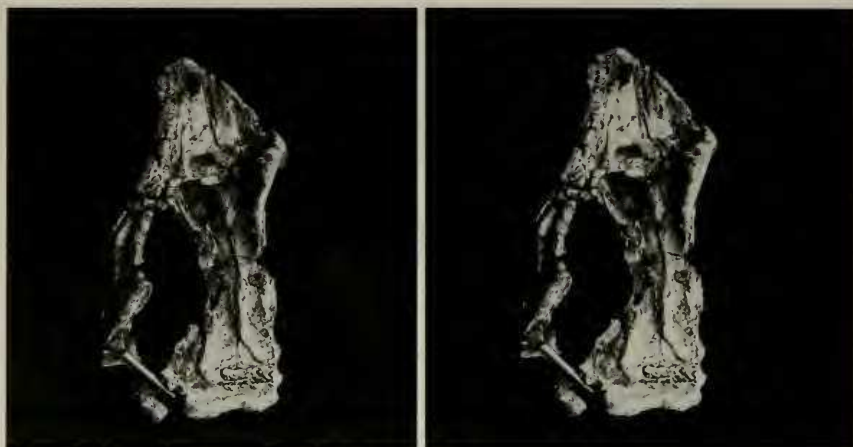
Figure 2.   *Therioherpeton cargnini*. Ventral view of the incomplete skull of the holotype. The secondary osseous palate shows an unossified area of the palatine. However, the posterior border of the right palatine is well preserved. Most of the ventral side of the skull roof from nasals to parietals is shown.

side of the rib cage of a rhynchosaur, probably *Scaphonyx* sp. (Schultz, 1986). All but six vertebrae are incomplete. Three cervicals are articulated in a small, isolated block, associated with the blade of the right scapula. The centra of these vertebrae are anteroposteriorly short, transversely wide, and dorsoventrally low, and have a wide neural canal. The inferred last cervical, articulated with a series of 15 dorsals (Fig. 5A), also has a short, wide, and dorsoventrally low centrum; the neural ca-

nal is wider than the centrum because the pedicles of the neural arch project dorsolaterally.

The anteroposterior lengths of the seven anterior dorsals gradually increase; neural canals remain very large (Fig. 5A). The 8th through 10th dorsals preserve the neural spines, which are posterodorsally inclined. The centra of the 11th through 14th dorsals are longer than those of preceding vertebrae; in these vertebrae, the large neural canal is formed in part by the ven-
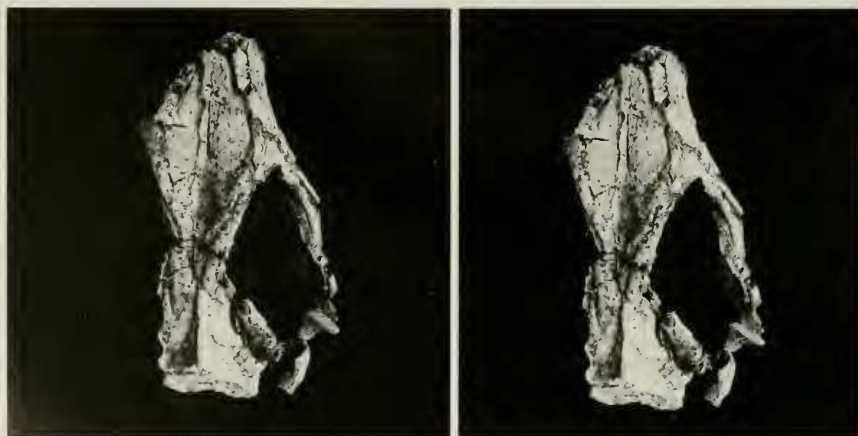

Figure 3.   *Therioherpeton cargnini*. Dorsal view of the incomplete skull of the holotype, showing the anterolateral projection of the frontals as well as their extensive, wedge-shaped posterior projection.
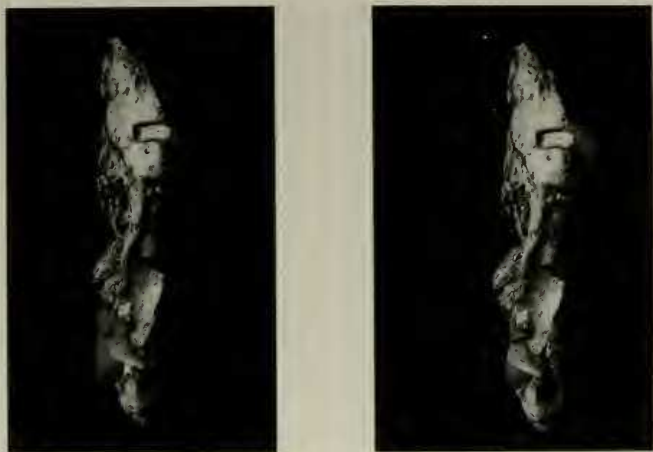
Figure 4. *Therioherpeton cargnini.* Right lateral view of the incomplete skull and jaw of the holotype. Note the slender zygomatic section of the jugal, and the incipiently bifurcated root of Pc[5].

tromedial surfaces of the neural pedicles that contribute to the floor of the neural canal. The number of dorsal vertebrae is uncertain because of a gap between the fifteenth dorsal and the next group of vertebrae. The zygapophyses of the last dorsal vertebrae are anteroposteriorly robust and oriented almost horizontally, with little inclination toward the median plane. The vertebrae forming the sacrum are difficult to discern individually, although one bears fragments of sacral ribs. We infer that there might be three or possibly four sacral vertebrae. All are rather robust, and the neural canals are as wide as the centra.

Subcylindrical fragments (and many molds) preserve 15 incomplete ribs on the right side and 17 on the left side (Figs. 5A, 6). There is no evidence of overlapping uncinate processes as are known in many cynodonts. Cervical ribs, which are short, thick, and posteriorly deflected, articulate behind the anterior margins of the centra, not between adjacent centra as in *Thrinaxodon liorhinus* (Jenkins, 1971). The dorsal ribs, which in cross section are figure 8–shaped, exhibit no clear indication of a lumbar region, except that the posterior dorsal ribs gradually decrease in length.

The pectoral girdle is represented only by the blade of the right scapula (not fully prepared at present). The anterior and posterior borders of the blade project laterally, forming a deep sulcus for musculus supracoracoideus, similar to the condition in *Thrinaxodon liorhinus* (Jenkins, 1971). The distal half of the right humerus is preserved, and appears to be relatively primitive by virtue of its great distal width and the presence of an ectepicondylar foramen. The ?right radius and ulna are incompletely preserved and reveal no diagnostic characters.

Of the two incomplete ilia, the left ilium (Fig. 5B) preserves part of the blade, which has almost parallel dorsal and ventral borders and lacks a posterior process. The lateral aspect of the blade is dorsoventrally convex. The pubic pedicle is more developed and stronger than the area of ischial contact. The ischium (Fig. 5D) has an elongate, narrow neck, and forms with the pubis a large obturator fenestra. The pubis (Fig. 5C) exhibits a well-defined, "twisted" neck below the acetabulum. A thickening of the anterior margin of the pubis ventral to the neck represents a pubic process. The inferior border of the pubic ramus is rather straight, whereas the superior border is concave and forms part
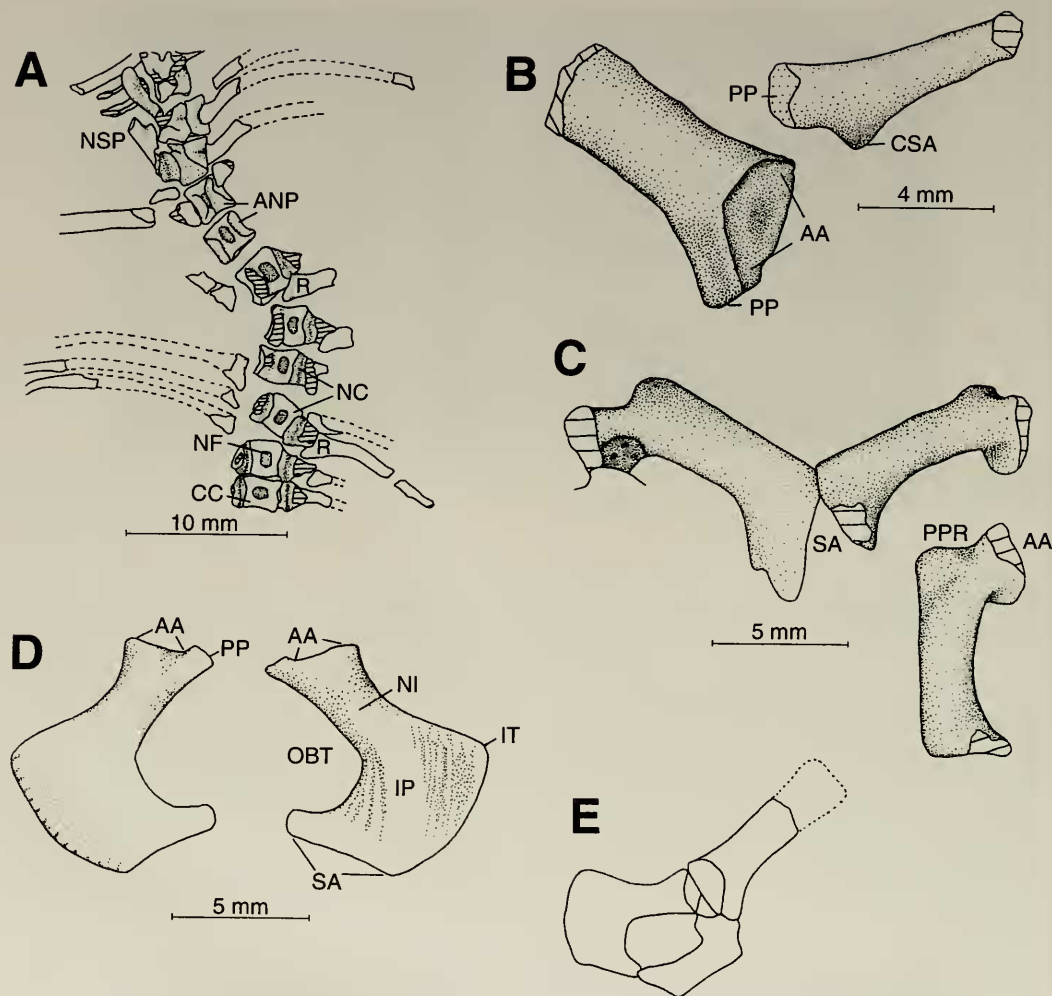
Figure 5.   *Therioherpeton cargnini.* (A) Sequence of articulated incomplete vertebrae and ribs from the putative last cervical (at the bottom) to the 10th dorsal. (B) Incomplete left ilium in lateral (left) and ventral (right) views. (C) Both pubes in dorsal view as preserved, and the left pubis in lateral view. (D) Right ischium in lateral (left) and medial (right) views. (E) Reconstruction of the right half of the pelvis in lateral view. *Abbreviations:* AA, acetabular area; ANP, area for neural pedicles; CC, cervical centrum; CSA, crista supracetabularis; IP, ischial plate; IT, ischial tuberosity; NC, neural canal; NF, neural fossa; NI, neck of the ischium; NSP, neural spine; OBT, obturator foramen; PP, pubic pedicle; PPR, pubic process; R, rib; SA, symphysial area.

of the margin of the large obturator fenestra.

The left femur is nearly complete (Figs. 7A, 8). The proximal end gradually expands mediolaterally, and the trochanters are less defined than in *Oligokyphus* (Kühne, 1956) and *Morganucodon* (Jenkins and Parrington, 1976). The femoral head is anteromedially and somewhat dorsally directed, although the precise orientation is obscured by slight deformation. The proximally positioned lesser trochanter is similar to that of *Oligokyphus* and *Morganucodon*, and different from the more ventrally placed trochanters of *Probelesodon* (Romer and Lewis, 1973), *Massetognathus* (Jenkins, 1970), and *Exaeretodon* (Bonaparte, 1963). The greater trochanter is

Figure 6.　*Therioherpeton cargnini.* Part of the presacral vertebral column showing broad neural arches, posterodorsally directed neural spines, and ribs without overlapping processes.
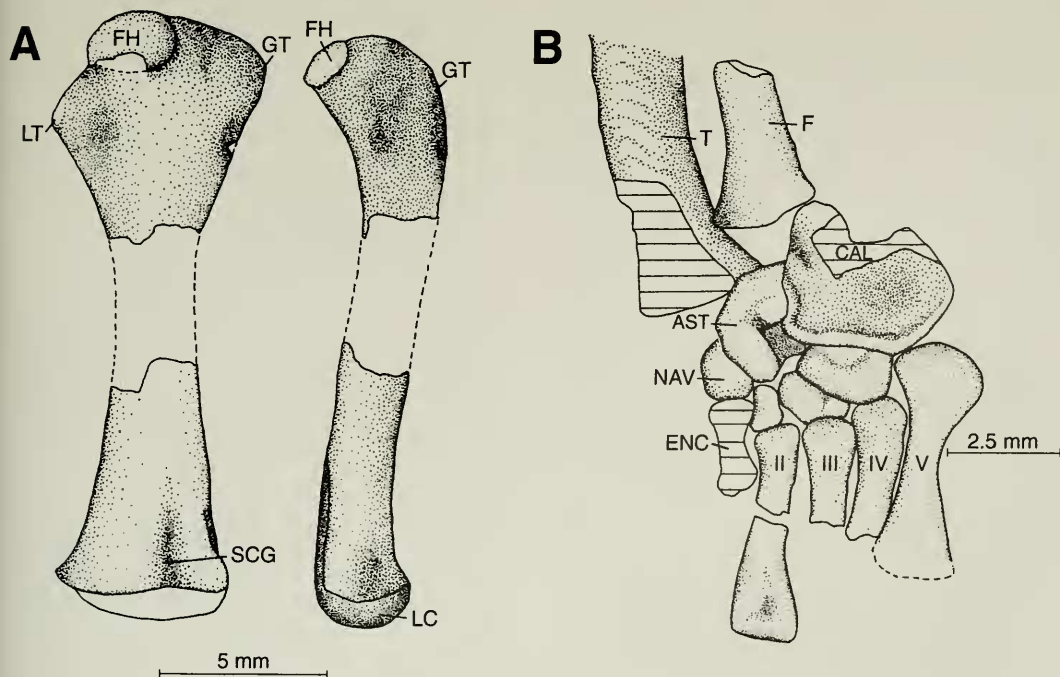

Figure 7.　*Therioherpeton cargnini.* (A) Left femur in anterior and lateral views. (B) Distal portions of right tibia and fibula articulated with the incomplete foot in plantar view. *Abbreviations:* AST, astragalus; CAL, calcaneum; ENC, entocuneiform; F, fibula; FH, femoral head; GT, greater trochanter; LC, lateral condyle; LT, lesser trochanter; NAV, navicular; SCG, supracondylar groove; T, tibia; II–V, metatarsals II through V.

Figure 8.   *Therioherpeton cargnini*. On the left is a series of incomplete sacrocaudal vertebrae in dorsal view. Also present are the left femur, left pubis, incomplete left ilium, and incomplete left foot. The ilium rests on a rhynchosaur (*Scaphonyx* sp.) rib.

proximally positioned and is united with the femoral head by a thin lamina of bone. Morphologically, the greater trochanteric structure is similar to that of *Oligokyphus* and *Morganucodon*, and very different from the condition in *Cynognathus* (Jenkins, 1971), *Probelesodon* (Romer and Lewis, 1973), *Massetognathus* (Jenkins, 1970), and *Exaeretodon* (Bonaparte, 1963). The lateral femoral condyle has a larger radius of curvature than the medial; a shallow supracondylar groove is present on dorsal surface of the distal end.

The astragalus, which is larger than the calcaneum, is only partially superimposed on the latter (Fig. 7B). Inasmuch as the calcaneum is damaged along its proximal margin, the presence or absence of a calcaneal tuber cannot be determined. The relatively elongate, slender proportions of the metatarsals resemble those of *Oligo-kyphus* (Kühne, 1956), rather than those of *Exaeretodon* (Bonaparte, 1963) or "?*Aleodon*/?*Scalenodon*" (Jenkins, 1971).

A Summary of the Distinctive Features of Therioherpeton. Although *Therioherpeton* possesses many features that are found in other Triassic cynodont families, the following assemblage is characteristic only of *Therioherpeton* and represents the degree to which this taxon approaches the morganucodontid level of organization.

1) Absence of prefrontal and postorbital bones as well as a postorbital bar (also in tritheledontids and tritylodontids).
2) Frontal bordering the orbit (also in tritheledontids and tritylodontids).
3) Frontal with anterolateral projection in dorsal view, and an elongate posterior projection.
4) Large lacrimal (also in tritheledontids and tritylodontids).

Comment. The first three characters listed above differentiate *Therioherpeton* from the Thrinaxodontidae, Cynognathidae, Chiniquodontidae, and Probainognathidae. Some of the characters are shared with the Tritylodontidae (Kühne, 1956; Sun, 1984; Sues, 1985) and Tritheledontidae (Crompton, 1958; Bonaparte, 1980), but in tritylodontids the zygomatic arch is deep and the dentition very derived, whereas in tritheledontids the specialized incisors, reduced canines, and bulbous upper postcanines differ from the corresponding features in *Therioherpeton*. The upper postcanines of the tritheledontids are transversely expanded, whereas in *Therioherpeton* they are narrow, with the

cusps in line. The structure of the frontal resembles that of *Morganucodon* (Kermack et al., 1981) in the type of contact with the nasal, a possible result of the absence of the prefrontal, as well as in the long, tapering contact with the parietals.

5) Contact between the ventral process of frontal and dorsal process of palatine (also in tritheledontids and tritylodontids; and in *Probainognathus* and chiniquodontids; J. A. Hopson, personal communication).

6) Large infraorbital foramen and two well-defined foramina for the trigeminal nerve in the maxilla (also in tritheledontids and tritylodontids).

7) Carnivorous–insectivorous dentition, similar to that of *Thrinaxodon* and *Morganucodon*, but with upper postcanines without cingula and possessing incipiently bifurcated roots.

8) Articular process of the dentary posteriorly and transversely expanded, without indication of a condyle, and set at a higher level than the alveoli (a common feature in derived cynodonts; J. A. Hopson, personal communication).

9) Cervical centra anteroposteriorly short, transversely wide and dorsoventrally low (also in *Oligokyphus*, other tritylodontids, and *Morganucodon*).

10) Neural canal of presacral vertebrae wider than the centrum.

Comment. The neural canal in *Therioherpeton* is proportionally larger than that in most cynodonts with which we were able to make a comparison. Neural canal size in the cervical, thoracic, sacral, and proximal caudal vertebrae of *Oligokyphus* (Kühne, 1956) approaches that of *Therioherpeton*, but is nonetheless proportionally smaller. The neural canal of *Therioherpeton* is in fact almost identical in proportions to that in *Morganucodon* (Jenkins and Parrington, 1976).

11) Absence of anapophyses.

12) Ribs without expanded processes (also in *Exaeretodon*, chiniquodontids, *Probainognathus,* and tritylodontids; and in tritheledontids as well; J. A. Hopson, personal communication).

13) Neural spines of presacral vertebrae posterodorsally directed (also in tritylodontids).

Comment. Short, posterodorsally directed neural spines in the posterior dorsals are known only in *Oligokyphus* and *Therioherpeton.* In *Morganucodon,* the posterior dorsals bear vertical neural spines, with fully differentiated lumbar vertebrae. The similarities between some derived axial characters in *Oligokyphus* and *Therioherpeton* suggest the probability of parallel evolution.

14) Iliac blade with dorsal and ventral borders subparallel, without posterior process (also in some tritylodontids; and tritheledontids; J. A. Hopson, personal communication).

15) Lateral side of the iliac blade dorsoventrally convex (also in tritylodontids and tritheledontids; J. A. Hopson, personal communication).

16) Ischium with narrow neck posterior to the acetabulum, and a concave dorsal border (also in *Oligokyphus* and tritheledontids; J. A. Hopson, personal communication).

17) Large obturator fenestra (also in tritylodontids and tritheledontids; J. A. Hopson, personal communication).

18) Pubis narrow with reduced distal contact with the ischium (also in tritheledontids; J. A. Hopson, personal communication).

Comment. The available parts of the ilia, the complete pubes, and the ischium show that the pelvis of *Therioherpeton* is more derived than that in any known cynodont family except the Tritylodontidae (Kühne, 1956) and Tritheledontidae (J. A. Hopson, personal communication).

19) Greater trochanter at the same level as the femoral head (also in *Oligoky-*

phus and tritheledontids; J. A. Hopson, personal communication).

20) Elongate, slender metatarsals (also in *Oligokyphus*).

SYSTEMATIC PALEONTOLOGY

Therapsida Broom, 1905

Cynodontia Owen, 1861

Family Incertae Sedis

Genus *Prozostrodon* New Genus

Type species, *Prozostrodon brasiliensis* (Barberena, Bonaparte, and Sá Teixeira, 1987).
Synonymy *Thrinaxodon brasiliensis* Barberena, Bonaparte, and Sá Teixeira, 1987.

Holotype. PV 0248T, Department of Paleontology and Stratigraphy, Universidade Federal de Rio Grande do Sul, Brazil.

Etymology. The generic designation alludes to the cingula of lower postcanine teeth (Greek, *zoster,* a girdle or band), in combination with Latin, *pro-*, before, in reference to the hypothesized antecedant phylogenetic position of the taxon.

Revised Generic and Specific Diagnosis. Reduced prefrontal and postorbital; lacrimal with large dorsal exposure; pronounced posterodorsal process of the premaxilla between septomaxilla and maxilla. Posterior projection of the frontal shorter than in *Therioherpeton*; anterolateral process of the frontal shorter than in *Therioherpeton,* and contacts the posterolateral border of the nasal, as in *Therioherpeton* and *Morganucodon.* Frontal, palatine, and orbitosphenoid extensively contact one another in the orbital wall. Five conical upper incisors; four lower incisors slightly spatulate and procumbent (as in *Morganucodon*). Triconodontlike postcanines without well-defined cingula on the uppers (except for an incipient buccal cingulum on the distal upper postcanine, as in *Thrinaxodon liorhinus* and chiniquodontids); lingual cingula on lower postcanines bear up to nine small cusps (as in *Thrinaxodon liorhinus*). Length of lower tooth row more than half the length of the dentary (as in *Morganucodon*). Secondary bony palate extends posteriorly beyond the last upper postcanine, as in chiniquodontids and tritheledontids. Neural canal of the presacral vertebrae large (as in *Oligopkyphus*), but smaller than in *Therioherpeton.* Neural spines posterodorsally inclined (as in tritylodontids). Zygapophyses of posterior dorsal vertebrae anteroposteriorly elongated, with anterior and posterior facets that are transversely concave and convex, respectively. Ribs without expanded processes. Iliac blade with a vestigial posterior process and a convex lateral surface (as in *Therioherpeton* and tritylodontids; also in tritheledontids; J. A. Hopson, personal communication).

Horizon and Locality. Facies Alemoa of the Santa Maria Formation, 200 m northwest of the hill Cerriquito, in a road cut of route BR-216, Municipio of Santa Maria, State of Rio Grande do Sul, southern Brazil.

Age. Early Late Triassic.

Material. An incomplete skull lacking most of the parietal crest, the braincase, and zygomatic arch. The orbital, preorbital, and infraorbital regions, secondary bony palate, and upper dentition are nearly complete. The right dentary and dentition are complete; the left dentary also has a complete dentition but lacks the ascending ramus and articular process. The postcranium is represented by three incomplete presacral vertebrae, 14 dorsal centra, seven dorsal neural arches, several fragmentary ribs, interclavicle, incomplete right humerus, proximal half of the left humerus, incomplete right ilium, distal halves of both femora, and a disarticulated right foot.

Comments. Significant features of the skull have been more clearly exposed through recent preparation. The skull shows some postmortem cracking and distortion.

DESCRIPTION

Skull (Figs. 9–11). The prefrontal and postorbital are reduced, and there is no indication of a postorbital bar (Fig. 9). The
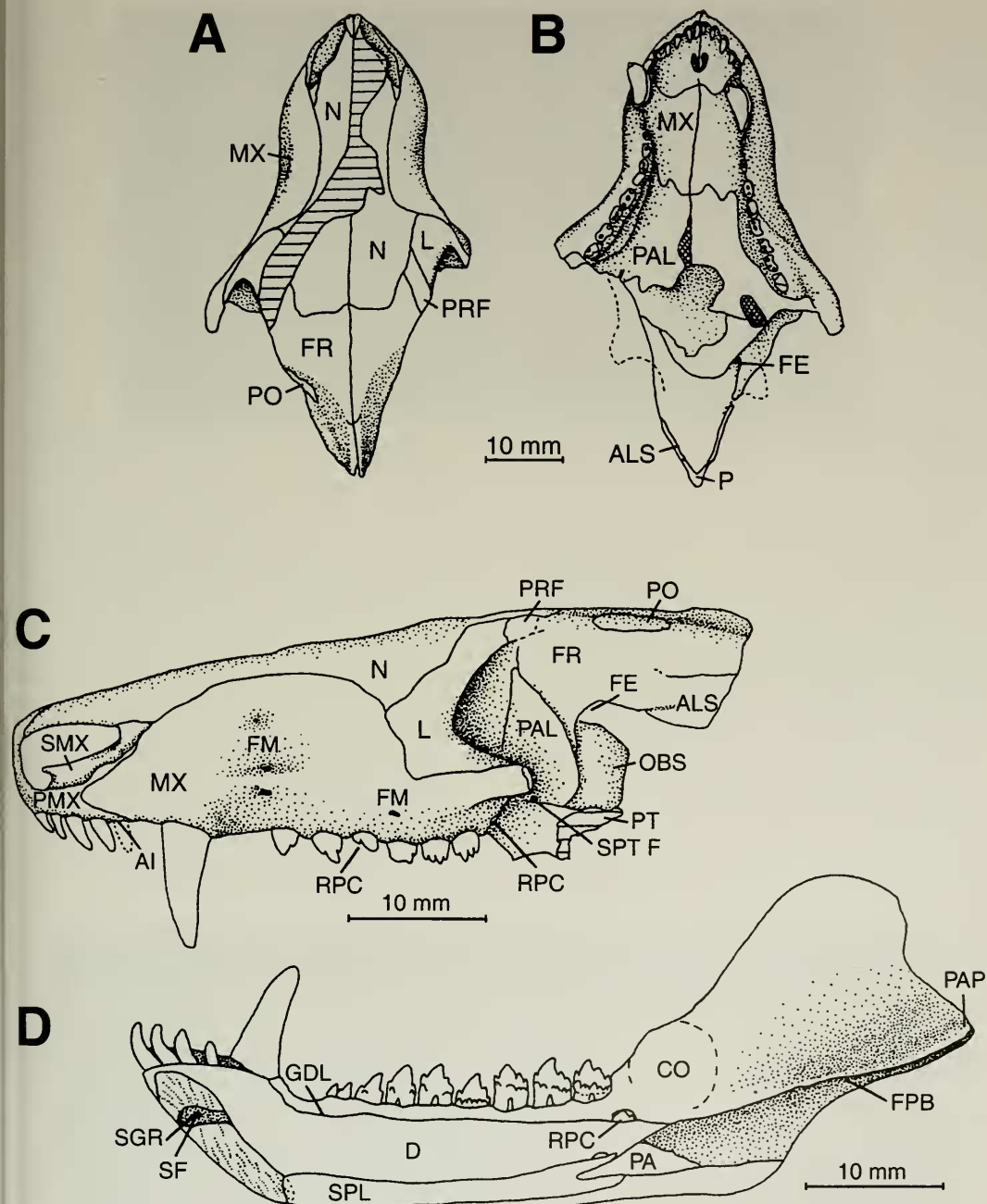
Figure 9. *Prozostrodon brasiliensis,* new genus. Incomplete skull in (A) dorsal, (B) ventral, and (C) left lateral views. (D) Incomplete right lower jaw in medial view. *Abbreviations:* AI, alveolus for incisor; ALS, alisphenoid; CO, coronoid; D, dentary; FE, ethmoidal foramen; FM, maxillary foramina; FPB, fossa for postdentary bones; FR, frontal; GDL, groove of dental lamina; L, lacrimal; MX, maxilla; N, nasal; OBS, orbitosphenoid; P, parietal; PA, prearticular; PAL, palatine; PAP, prearticular process; PRF, prefrontal; PMX, premaxilla; PO, postorbital; PT, pterygoid; RPC, replacing postcanine; SF, symphysial foramen; SGR, symphysial groove; SMX, septomaxilla; SPL, splenial; SPT F, sphenopalatine foramen.
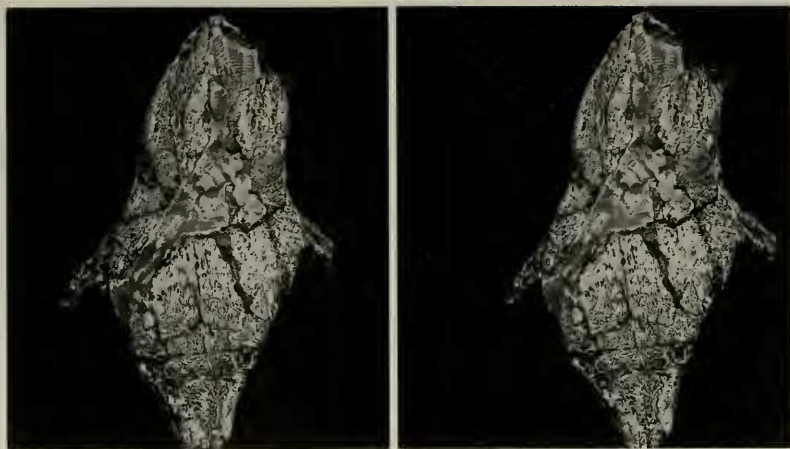
Figure 10.   *Prozostrodon brasiliensis,* new genus. Dorsal view of the holotype skull. The anterolateral projection of the frontal is shown.

frontal borders the orbit and extends anterolaterally to contact the lateral, posterior portion of the nasal, as in *Therioherpeton.* The orbital process of the frontal contacts the dorsal process of the palatine and the orbitosphenoid, similar to that of *Morganucodon* (Kermack et al., 1981, fig. 96). The sphenopalatine foramen in *Morganucodon* is bordered by the palatine and orbitosphenoid (Kermack et al., 1981), whereas in *Prozostrodon* it is entirely enclosed by the palatine, possibly the primitive condition, with the orbitosphenoid in

a more posterior position. Despite this difference, it is interesting to note the structural similarities of the interorbital regions of *Morganucodon* and *Prozostrodon,* with the exception that the distance between the ethmoidal foramen (Fig. 9C) and the anterior border of the orbit is proportionally shorter in *Morganucodon,* possibly representing a derived condition.

A small prefrontal is present (Fig. 9A), anteriorly reduced by the posterior expansion of the lacrimal. A small orbital process of the prefrontal is possibly present, con-
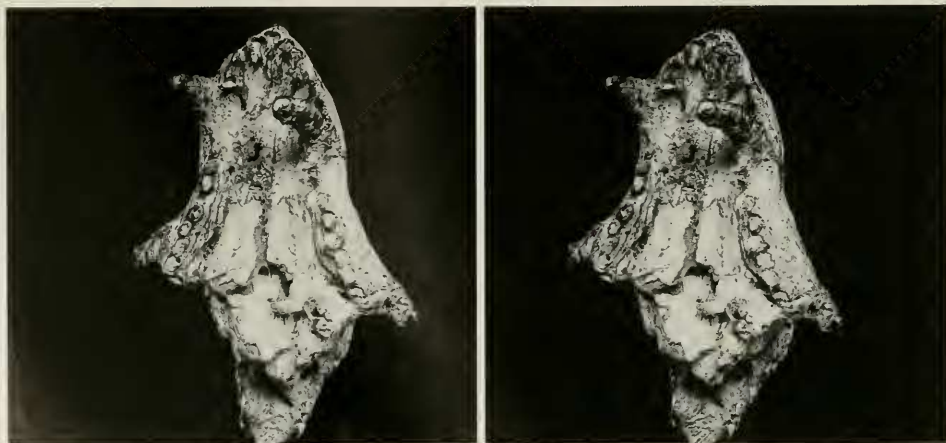

Figure 11.   *Prozostrodon brasiliensis,* new genus. Ventral view of the holotype skull.

tacting a similar process of the frontal, but it cannot be positively identified because the sutures are not clear.

The postorbital is represented only on the left side (Fig. 9C) as a small plate overlapping the frontal and parietal on their dorsolateral surfaces. The bone has some external sculpturing, but there is no indication of the postorbital bar.

The premaxilla has a narial process contacting the nasal (Fig. 9C). The lateral posterodorsal process contacting the maxilla is slender and is partially covered by the maxilla. The premaxilla has a long contact with the septomaxilla and does not reach the nasal.

The slender septomaxilla of *Prozostrodon* (Fig. 9C) appears similar to that of *Sinoconodon* (Crompton and Luo, 1993), although it is uncertain whether a septomaxillary foramen is present or not.

The rather large maxilla projects laterally over the premaxilla up to the level of the third incisor (Fig. 9C). A posterior process of the maxilla forms the anterior portion of the zygomatic arch. A large infraorbital foramen lies below the anterior margin of the lacrimal, and two well-defined maxillary foramina are present above the anterior border of the first postcanine.

The anteroposteriorly elongate palatines of *Prozostrodon* (Fig. 9B) resemble a similar configuration in the bony palate of chiniquodontids and morganucodontids. Although the posterior border of the right palatine is broken, the left side is completely preserved and extends posterior to the last postcanine; this condition is similar to that in *Probelesodon kitchingi* (Sá Teixeira, 1979) and trithelodontids, and is a little more extensive than in *Therioherpeton*. The posterior half of the secondary bony palate is widest posteriorly where the tooth row diverges posterolaterally. There is a deep sulcus along the palatine–maxilla suture to accommodate the crowns of the lower postcanines when the jaw is closed. Greater and lesser palatine foramina are present.

Upper Dentition. The upper dentition comprises five incisors, one canine, and seven postcanines (Fig. 9C). The incisors are slender and posteriorly recurved. All five incisors, which are slender and slightly recurved, are present on the right; four incisors and an alveolus for the fifth incisor are present on the left.

In right upper postcanine row, the third and seventh (last) teeth were in the process of erupting. Postcanine crowns are of the "triconodont" type, with cusps aligned mesiodistally. In the three posterior postcanines, four cusps (A, B, C, and D) are present. The labial side is mesiodistally convex, whereas the lingual face is rather concave or flat, with some ill-defined wear; the lack of well-defined facets suggests that no precise occlusion was present. The mesiolingual corner of the last left postcanine bears a poorly defined, low cusp in a position that might be expected of an incipient lingual cingulum. Conversely, the last right postcanine (in the process of erupting) bears a small buccal cusp distally; there is no indication of buccal cingular development in the functional postcanines. The occurrence of cingular cuspules only on the last upper postcanine in *Prozostrodon* is perhaps comparable to the condition in *Thrinaxodon liorhinus* (Osborn and Crompton, 1973; also suggested for *Pachygenelus*; Gow, 1980) in which morphological complexity increases towards the distal end of the tooth row. The roots of the upper postcanines show evidence of incipient bifurcation, as originally indicated by Barberena et al. (1987).

Lower Jaw and Dentition (Figs. 9D, 12). The dorsal and ventral margins of the elongate body of the mandible (Fig. 9D) are subparallel as far forward as the posterior border of the symphysis. Anterior to this point, the dentary extends anterodorsally, elevating the alveolar plane of the incisors and canine above that of the postcanines.

The articular process is transversely expanded, mostly medially, without evidence of an articular condyle. The posteroventral angle of the dentary is broadly convex,
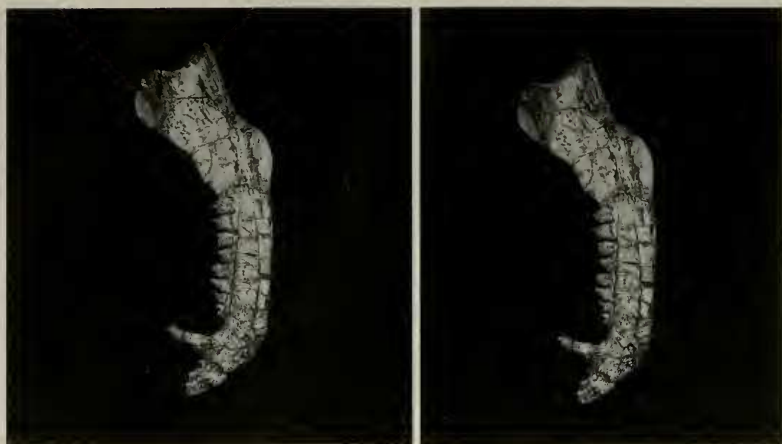
Figure 12.   *Prozostrodon brasiliensis,* new genus. Right lower jaw of the holotype in medial view. Note the incipiently bifurcated postcanine roots.

lacking a posteriorly projecting angular process. A coronoid is probably present, largely fused to the medial side of the ascending ramus. The unfused symphysis exhibits rugosity indicative of ligamentous insertion, and a symphysial fossa and foramen as in *Cynognathus* (Kermack et al., 1973).

The lower dentition consists of four incisors, one canine, and 10 postcanines (Barberena et al., 1987). The incisors are slightly procumbent and recurved, with some mesiodistal expansion of the crown in the first three. The fourth incisor is shorter, mesiodistally narrow, and separated from the canine by a short diastema.

The well-preserved postcanines become more complex toward the back (as is common in carnivorous–insectivorous cynodonts; Osborn and Crompton, 1973) as well as increase in size. The following account is based on the right postcanines. Lower postcanine 1 is small, conical, and without accessory cusps. Lower postcanine 2 bears a large main cusp a with smaller cusps b (mesially) and c (distally). A slight lingual cingulum is present. On Pc_3, cusp a has a sharp distal edge, and cusps b and c are positioned on the buccal half of the tooth. Incipient division of the root is apparent in buccal aspect. Lower postcanine

4, substantially larger than preceding postcanines and also exhibiting incipient root division, possesses a (broken) lingual cingulum and a mesial and distal lingual cuspule. Lower postcanine 5 is mesiodistally longer than Pc_4 and has larger accessory cusps b and c. The lingual cingulum is not continuous mesiodistally, but has anterior and posterior sections, each bearing a cuspule. The base of the crown is larger than the root, which is well differentiated from the crown and exhibits a vertical groove. Lower postcanine 6, which is almost fully erupted, bears a conical, recurved cusp a, and a cusp d on the distal margin. Cusp c is larger than cusp b. The cingulum, which is more developed than in the preceding postcanines, extends along most of the lingual side and bears six cuspules. Cusp a is broken on Pc_7, but cusps b, c, and d are present and aligned with the base of cusp a. The lingual cingulum is continuous. The occlusal surface of the cingulum and the surface above it suggest abrasion by food while chewing. The root is deeply grooved. Lower postcanine 8 is complete, with basically the same features as in Pc_7. Lower postcanine 9, mesiodistally the longest postcanine, has a proportionally lower crown as well as the lowest cusp a (on the left side, Pc_9 appears to be in the final
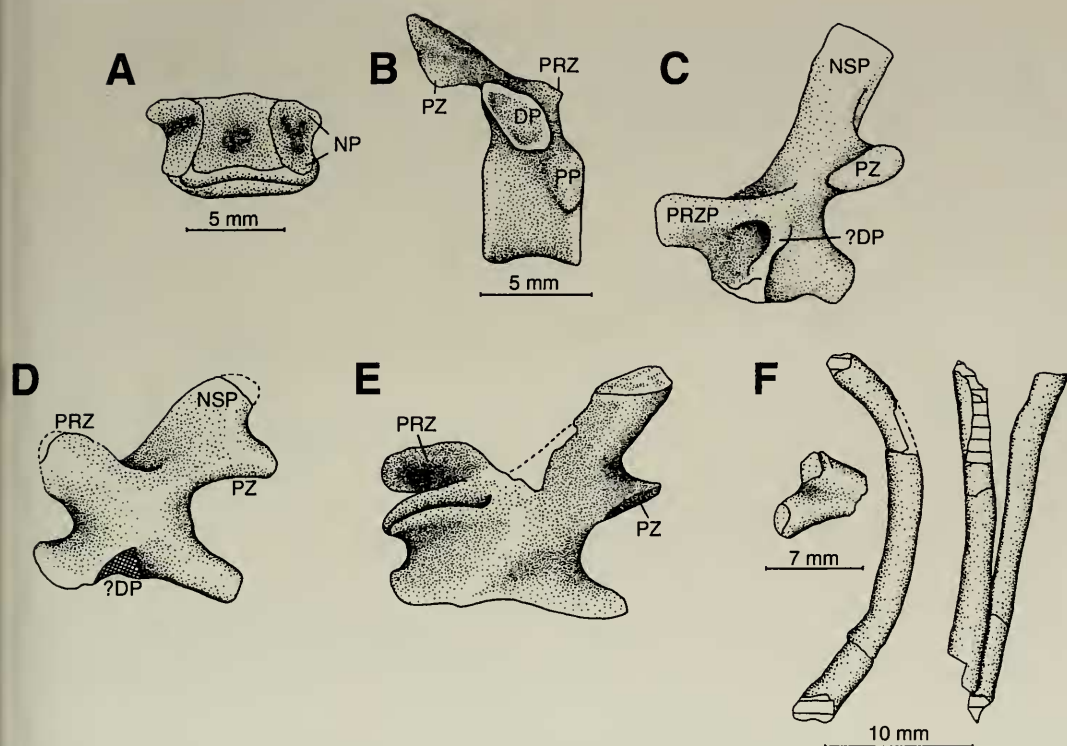
Figure 13. *Prozostrodon brasiliensis,* new genus. (A) Cervical centrum in dorsal view. (B) Anterior dorsal vertebra in lateral view. (C, D, E) Lateral views of three neural arches from the dorsal series. (F) Incomplete ribs. *Abbreviations:* DP, diapophysis; ?DP, ?diapophysis; NP, contact for neural pedicle; NSP, neural spine; PP, parapophysis; PRZ, prezygapophysis; PZ, postzygapophysis; PRZP, prezygapophysial process.

stage of eruption). Seven small cusps form the lingual cingulum. The degree of incipient root bifurcation is greater than in preceding postcanines, representing a morphological gradient that is also expressed in the increasing complexity of the cingula. The right Pc_{10} is unerupted; cusp a and part of c are exposed just below the groove for the dental lamina. The left Pc_{10} is just beginning to erupt; the position of this tooth distal to the end of the alveolar row is evidence that the individual was still growing.

Postcranium. One centrum (Fig. 13A) is tentatively considered to be cervical because it is transversely wide and anteroposteriorly short, as are the cervicals of *Therioherpeton.* The facets for the pedicles of the neural arch are in a dorsolateral position; if the pedicles were to have pro-

jected dorsolaterally, the neural canal would have been relatively wide. The parapophyseal facets are located entirely on the anteroventral margin of the centrum; there is no indication that rib heads spanned adjacent vertebrae.

A nearly complete anterior dorsal vertebra (Fig. 13B) exhibits a parapophysis on the dorsolateral region of the centrum, a large diapophysis that projects laterally from the middle of the pedicle, and a neural spine that is directed posterodorsally. The centrum is moderately amphicoelous. The neural canal is large but narrower than the centrum, differing in this respect from *Therioherpeton* (and possibly reflective of the more adult stage of *Prozostrodon*; J. A. Hopson, personal communication).
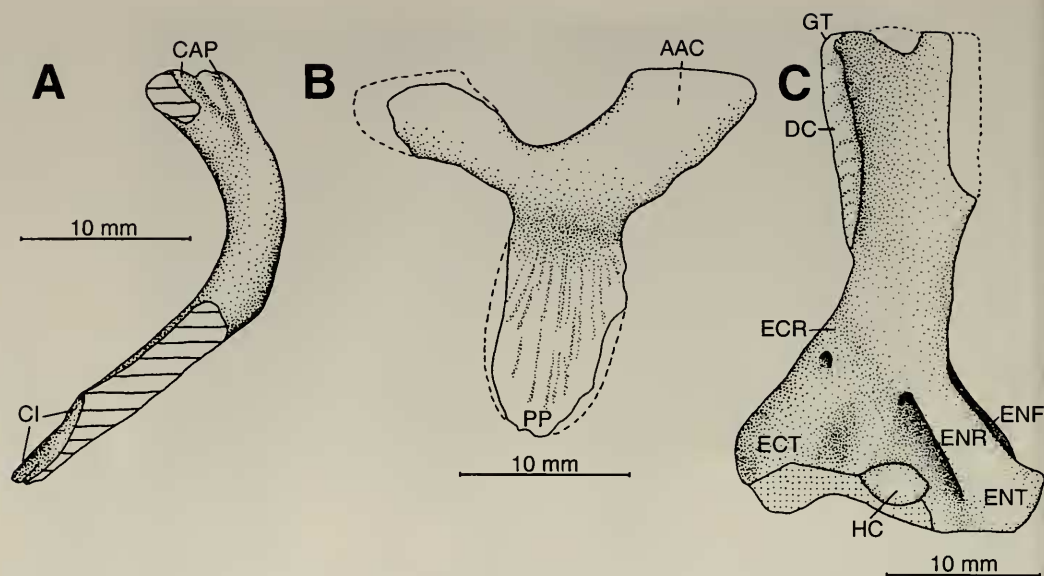
The dorsolumbar region is further rep-

Figure 14.   *Prozostrodon brasiliensis,* new genus. (A) ?Right clavicle in ?posterior view. (B) Interclavicle in dorsal view. (C) Right humerus in ventral view. *Abbreviations:* AAC, attachment area for right clavicle; CAP, contact with acromial process; CI, contact with interclavicle; DC, deltopectoral crest; ECT, ectepicondyle; ECR, ectepicondylar ridge; ENF, entepicondylar foramen; ENR, entepicondylar ridge; ENT, entepicondyle; GT, greater trochanter; HC, humeral capitulum; PP, posterior projection.

resented by an incomplete vertebra and four incomplete neural arches. The former has a massive centrum with marked amphicoely. The transverse processes are directed laterally and the broken base of the neural spine indicates that the spine was directed posterodorsally. The neural canal is large but narrower than the centrum. Structural variations in the spinous processes and zygapophyses are evidence of regional variation along the dorsolumbar column.

In one neural arch (Fig. 13C), the robust prezygapophyses are positioned more ventrally than the postzygapophyses; postzygapophyseal facets are anteroposteriorly elongate and transversely convex, possibly representing a specialization for dorsoventral flexure of the vertebral column (J. A. Hopson, personal communication). The neural spine, with almost parallel anterior and posterior borders, is posterodorsally directed, and more steeply inclined than in *Exaeretodon* (Bonaparte, 1963). Another neural arch (Fig. 13E) has

a similarly elongate set of postzygapophyses with convex facets, and prezygapophyses with transversely concave facets. Jenkins and Parrington (1976, figs. 2A–D) illustrated a neural arch in *Morganucodon* with zygapophyses and a neural spine of comparable structure.

A different type of dorsal vertebra (Fig. 13D), represented by two neural arches, possibly derives from a position posterior to those described above. The zygapophyseal facets have less curvature and the damaged neural spine appears to be shorter than in the previously described neural arches.

Ribs (Fig. 13F). Eight to 10 ribs are represented by 20 fragments, and none show any indication of processes or expansions. Most are figure 8–shaped in cross section.

Clavicle (Fig. 14A). Most of the ?right clavicle is present. On the proximal end are furrowlike rugosities representing the area of attachment with the interclavicle. The wide distal end is complexly configured with surfaces representing the acro-

mial attachment. The greatest curvature of the shaft is closer to the distal end.

Interclavicle (Fig. 14B). This Y-shaped element, with broad anterolateral extensions for reception of the clavicles, is anteroposteriorly shorter (19 mm) than wide (23 mm). The ventral surface is not exposed.

Scapulocoracoid. These bones are represented only by small fragments that are too fragmentary to provide useful information on the glenoid and other features of interest.

Humerus (Fig. 14C). The left humerus is represented by the proximal half, including the deltopectoral crest and the humeral head. The right humerus is almost complete, lacking only the humeral head and part of the proximal end, and a small portion of the distal end including the articular surface for the ulna. The humerus is structurally no more derived than that of *Exaeretodon*, and is similar to that of *Probelesodon lewisi* (Romer and Lewis, 1973). The entepicondylar foramen is very large, and opens distally into a deep sulcus that continues to the entepicondylar terminus. The entepicondyle, which is larger than the ectepicondyle, terminates in a distinct projection. Near the anterior margin that extends proximally from the ectepicondyle is a small ectepicondylar foramen; this margin extends farther proximally onto the diaphysis than does the comparable margin from the entepicondyle.

Ilium (Fig. 15A). The right ilium is almost complete except for the most anterior end of the iliac blade. The neck above the acetabulum is well defined, and the posterior end of the iliac blade bears a very short process. Both of these features are derived compared with the structure seen in *Thrinaxodon* and *Cynognathus* (Jenkins, 1971) and in *Exaeretodon* (Bonaparte, 1963). The outer surface of the iliac blade is largely convex dorsoventrally, not concave as in the above cited cynodonts, and its dorsal and ventral borders are nearly parallel to one another.

Foot (Figs. 15B, C). The right hind foot

is complete, except for the lateral part of the calcaneum. The superposition of astragalus and calcaneum appears to be of the type present in *Exaeretodon* (Bonaparte, 1963), defined by Jenkins (1971) as the "therapsid type of plantigrady." However, the metatarsals and phalanges are proportionally longer than in *Exaeretodon*. The phalangeal formula is 2-3-3-3-3.

Comparison of Prozostrodon *with other Cynodonts.* The referral of PV 0248T to the genus *Thrinaxodon* by Barberena et al. (1987) is untenable, as pointed out by Battail (1991), who interpreted the specimen as a chiniquodontid. The following derived characters present in the holotype of *Prozostrodon brasiliensis* are not found in specimens of *Thrinaxodon* from the Early Triassic of South Africa (Parrington, 1946; Estes, 1961) and Antarctica (Colbert and Kitching, 1977).

1) Frontal bordering the orbit (also in *Therioherpeton*, tritheledontids, and tritylodontids).
2) Contact between the ventral process of frontal and dorsal process of palatine (also in tritheledontids and tritylodontids; additionally present in *Probainognathus, Ecteninion*, and chiniquodontids; J. A. Hopson, personal communication).
3) Presence of an orbitosphenoid contacting frontal and palatine, and medially placed relative to the dorsal process of the palatine (also in *Morganucodon*; Kermack et al., 1981).
4) Secondary bony palate with large palatines that extend to the level of the last postcanine.
5) Incipient bifurcation of the roots in the upper and lower postcanines.
6) Small postorbital and prefrontal.
7) Absence of postorbital bar (also in *Therioherpeton*, tritheledontids, and tritylodontids).
8) Large infraorbital and two well-defined foramina for the trigeminal nerve in the maxilla (also in tritheledontids and tritylodontids).
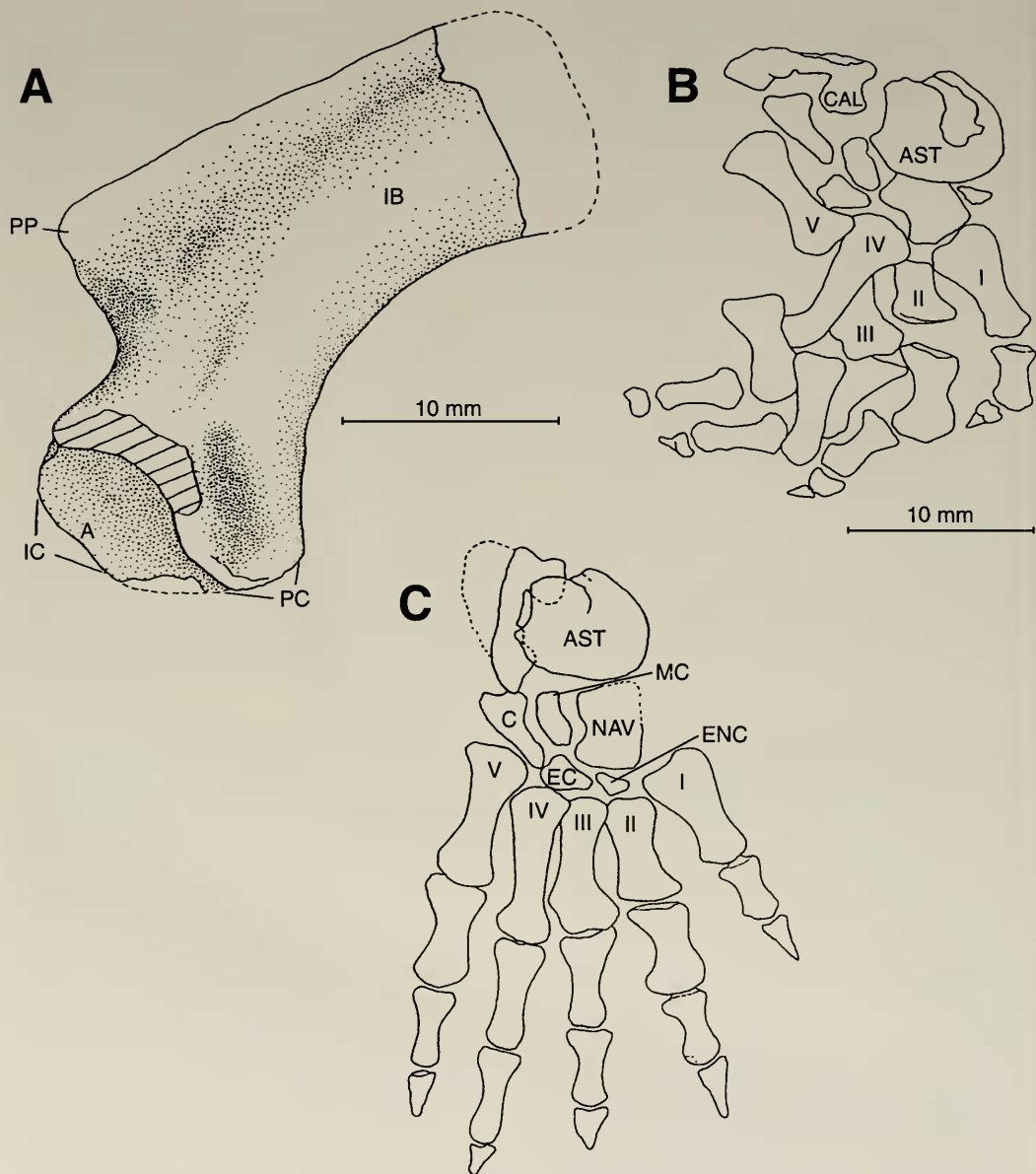
Figure 15. *Prozostrodon brasiliensis*, new genus. (A) Incomplete right ilium in lateral view. (B) Right foot as preserved. (C) Reconstruction of right foot in dorsal view. *Abbreviations:* A, acetabular area; AST, astragalus; CAL, calcaneum; C, cuneiform; EC, ectocuneiform; ENC, entocuneiform; IC, ischial contact; IB, iliac blade; MC, mesocuneiform; NAV, navicular; PC, pubis contact; PP, posterior process of the ilium; I–V, metatarsals I through V.

This combination of derived characters precludes referral of *Prozostrodon brasiliensis* not only to the Thrinaxodontidae, but also to the Cynognathidae, Chiniquo-dontidae, and Probainognathidae. The lack of gliriform specialization in the incisors and the transversely narrow postcanines preclude referral of the specimen to the

Tritheledontidae or to any gomphodont family, including the Tritylodontidae.

A *Summary of the Distinctive Features of* Prozostrodon. In addition to the characters listed above as well as in the diagnosis, *Prozostrodon* possesses other distinctive features. Although many of these features may be found among various other taxa, only in *Prozostrodon*, as far as we are aware, do they occur together. The suite is as follows.

1) Reduced unossified area between frontal, orbitosphenoid, and alisphenoid (also in tritylodontids and *Ecteninion*; Martínez et al., 1996).
2) Sphenopalatine foramen within the posterior portion of the dorsal process of palatine.
3) Anteroposteriorly long palatines in the secondary bony palate (also in chiniquodontids, tritheledontids, and some tritylodontids).
4) Root of the zygomatic arch distinctly offset from the posterior margin of the maxilla (also in *Probainognathus*, chiniquodontids, tritylodontids, traversodontids, and diademodontids).
5) Carnivorous–insectivorous dentition comparable in general morphology to that of *Thrinaxodon* and *Morganucodon,* but with cingula on the upper postcanines that are either poorly developed or absent altogether.
6) Posterior portion of the upper tooth row inset from the lateral border of the maxilla (also in traversodontids, tritylodontids, tritheledontids, and *Probainognathus*).
7) Incipient bifurcation of the upper postcanine roots.
8) Incipient bifurcation of the lower postcanine roots (also in *Pachygenelus* and *Microconodon*; H.-D. Sues, personal communication; and in *Therioherpeton*).
9) Mandibular symphysis unfused, anteroposteriorly elongated, dorsoventrally narrow (as in *Thrinaxodon* [primitive], tritheledontids, and trity-

lodontids [derived]; J. A. Hopson, personal communication).
10) Presence of symphysial fossa and foramen in the lower jaw (also in *Cynognathus*; Kermack et al., 1973).
11) Articular process of the dentary extended posteriorly and expanded transversely, without indication of a condyle, and set above the level of the postcanine teeth (a feature of derived cynodonts; J. A. Hopson personal communication).
12) Cervical centra anteroposteriorly short, transversely wide, and dorsoventrally low (also in tritylodontids and *Morganucodon*).

DISCUSSION

The specimens of *Therioherpeton* (skull length, 38 mm) and *Prozostrodon* (skull length estimated to be 67 mm) are relatively small, and consideration should be given to whether the smaller of the two represents a juvenile individual. Four features of *Therioherpeton*, in comparison to those in *Prozostrodon*, might be interpreted as evidence of immaturity: the frontals extend further posteriorly; the anterior portion of the braincase is proportionally wider; the postcanines lack cingula; the neural canals of presacral vertebrae are proportionally larger. However, the possibility that these are juvenile characters is contradicted by the state of ossification in the postcranium of *Therioherpeton*. With the exception of the pelvis, in which the three elements are not synostosed, we find no evidence of a subadult condition. Furthermore, *Therioherpeton* does not exhibit the proportionately large orbital size that is characteristic of juvenile individuals. A juvenile skull of cf. *Probainognathus* (Bonaparte and Crompton, 1994, figs. 1, 2) of comparable length (39 mm) to that of *Therioherpeton* exhibits a skull to orbit ratio of 3.5, versus an estimated 5.0 for *Therioherpeton*. In a putatively mature skull of *Probainognathus* (Romer, 1970, fig. 2) the ratio of skull to orbital length is 6, only slightly greater than in *Therioherpeton*. Al-
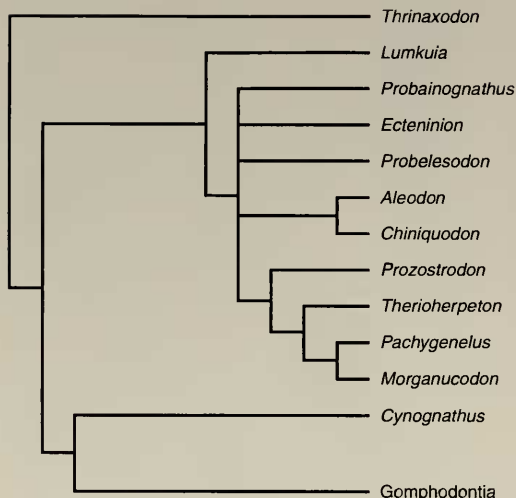
Figure 16.   The hypothesized phylogenetic positions of *Therioherpeton* and *Prozostrodon*. The cladogram was generated by Dr. J. A. Hopson, who incorporated information from the Brazilian genera described in this paper into his data set of cynodont characters.

though we do not believe that the type of *Therioherpeton* represents a juvenile, we remain open to the possibility that the four characters cited above eventually might be shown to be juvenile characters retained in adulthood.

The hypothesized relationships of *Therioherpeton* and *Prozostrodon* are depicted in Figure 16. The relative positions in the cladogram of the two genera seem due to the persistence of a prefrontal and postorbital and the shorter posterior projection of the frontal in *Prozostrodon,* and to the more derived characters present in the pelvis and proximal femur of *Therioherpeton.*

The materials of *Therioherpeton* and *Prozostrodon,* although incomplete, provide new anatomical information to further elucidate the complex transition between cynodonts and primitive mammals. The taxa described here support the hypothesis that the ancestry of mammals lay among the clade of carnivorous–insectivorous cynodonts (Hopson, 1991, 1994; Hopson and Kitching, 2001), rather than among gomphodont cynodonts, and in

particular the Tritylodontidae (Kemp, 1982, 1983). Sues (1985) reviewed in detail most of the synapomorphies that Kemp (1982, 1983) proposed in support of his interpretation that tritylodontids and primitive mammals were closely related, and concluded that many of these purportedly shared derived features are either superficial similarities, are symplesiomorphic, or are the result of parallel development but which, nonetheless, evidence structural differences.

We regard the dentition of *Prozostrodon* as morphologically intermediate between that of *Thrinaxodon liorhinus* from the Early Triassic and those evolved among Late Triassic and Early Jurassic morganucodontids. Although tritheledontids such as *Pachygenelus* have been considered as closely related to mammals (Hopson and Barghusen, 1986), and are represented cladistically as the sister taxon to mammals (Fig. 16; see also Shubin et al., 1991), we interpret the tritheledontid dentition as derived, particularly with respect to the buccolingual expansion of the upper postcanines. In contrast, the entire dentition of *Prozostrodon* (and what is known of that of *Therioherpeton*) is substantially similar to that in morganucodontids, with only slight differences in the development of upper postcanine cingula. During a span of time that witnessed major modifications in cranial and postcranial morphology, dental patterns were fundamentally conserved.

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